Controlling Factors of Feed Intake and Salivary Secretion in Goats Fed on Dry Forage

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ABSTRACT : The purpose of this research was to determine whether or not feeding induced hypovolemia (decreases in plasma volume) and decreases in plasma bicarbonate concentration caused by loss of $NaHCO_3$ from the blood, act to suppress feed intake and saliva secretion volumes during the initial stages of feeding in goats fed on dry forage. The animals were fed twice a day at 10:30 and at 16:00 for 2 h each time. Prior to the morning feeding, the collected saliva (3-5 kg) was infused into the rumen. During the morning 2 h feeding period (10:30 to 12:30), the animals were fed 2-3 kg of roughly crushed alfalfa hay cubes. At 16:00, the animals were fed again with 0.8 kg of alfalfa hay cubes, 200 g of commercial ground concentrate and 20 g of sodium bicarbonate. In order to compensate for water or $NaHCO_3$ lost through saliva during initial stages of feeding, a 3 h intravenous infusion (17-19 ml/min) of artificial mixed saliva (ASI) or mannitol solution (MI) was begun 1 h prior to the morning feeding and continued until the conclusion of the 2 h feeding period. The physiological state of the goats in the present experiment remained unchanged after parotid gland fistulation. Circulating plasma volume decreases caused by feeding (estimated by increases in plasma total protein concentration) were significantly suppressed by the ASI and MI treatments. During the first 1 h of the 2 h feeding period, plasma osmolality in the ASI treatment was the same as the NI (non-infusion control) treatment, while plasma osmolality in the MI treatment was significantly higher. In comparison to the NI treatment, cumulative feed intake levels for the duration of the 2 h feeding period in the ASI and MI treatments increased markedly by 56.6 and 88.3%, respectively. On the other hand, unilateral cumulative parotid saliva secretion volume following the termination of the 2 h feeding period in the ASI treatment was 50.7% higher than that in the NI treatment. MI treatment showed the same level as the NI treatment. The results of the present experiment proved that the humoral factors involved in the suppression of feeding and saliva secretion during the initial stages of feeding in goats fed on dry forage, are feeding induced hypovolemia and decrease in plasma HCO_3^- concentration caused by loss of $NaHCO_3$ from the blood. ***(Asian-Aust. J. Anim. Sci. 2005. Vol 18, No. 10 : 1414-1420)***

Key Words : Hay, Saliva Secretion, Hypovolemia, Plasma Bicarbonate, Goats

INTRODUCTION

Ruminants can consume large amounts of feed quicker than their non-ruminant counter-parts (Tsuda, 1994). These actions are supported by their salivary secretion pattern. Saliva secretion volumes in ruminants increase considerably during the initial stages of feeding, before decreasing to minimum levels that are continuously maintained (Sunagawa et al., 2002b; 2003). Saliva in ruminants consists mainly water and $NaHCO_3$. The water in the saliva acts as a lubricant in the mouth and esophagus, and assists in the mastication, regurgitation, and swallowing of dry forage. The water also supplies fluid to the non-secretory rumino-reticulum and helps facilitate mixing of the ruminal content. The sodium bicarbonate in the saliva being an alkaline, serves to buffer the decrease in the pH due to volatile fatty acid production in the rumen. In this way, saliva plays an important role in eating and homeostatic regulation of the acid-base balance in rumen fluid.

When sheep commence feeding, they secrete large volumes of both mixed saliva and parotid saliva (Sasaki et al., 1974; Sato, 1975). Saliva is produced from components in the blood and thus, at the onset of feeding, large amounts of water and $NaHCO_3$ move from the circulation into the rumen in the form of saliva. As a result, decreases in circulating plasma volumes, plasma HCO_3^- concentrations, and blood pH are observed in ruminants during the initial stages of dry forage feeding (Blair-West and Brook, 1969; Sasaki et al., 1975). On the other hand, in goats fed twice a day on roughly crushed alfalfa hay cubes, eating rates peaked 10 min after the start of feeding but rapidly decreased by the time 30 min of the feeding period had elapsed (Sunagawa et al., 2003). Parotid saliva secretion rates peaked immediately after commencement of feeding but decreased sharply to low levels from 30 min after feeding commencement (Sunagawa et al., 2003). However, little attention has been given to whether or not the changes observed in humoral parameters during the initial stages of feeding influence feed intake and saliva secretion volumes. It is hypothesized that the decrease in circulating plasma volumes and HCO_3^- concentrations caused by dry forage intake in ruminants, control feed intake and saliva secretion volumes. In order to prove this hypothesis, in goats fed roughly crushed alfalfa hay cubes twice a day, water and $NaHCO_3$ lost in the form of saliva, were replenished by way of intravenous infusion of artificial mixed saliva and mannitol solution. Observations were made as to whether or not this brought about an easing of the restriction of eating

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Table 1. Chemical composition and ingredients of alfalfa hay cubes and ground concentrate feed

	Alfalfa hay cubes	Ground concentrate feed
Dry matter (%)	84.3	86.9
Chemical composition (% of DM)		
Crude protein	18.7	13.4
Crude fat	2.4	3.6
Crude fiber	29.7	3.7
Nitrogen-free extracts (NFE)	39.7	71.0
NDF	45.9	14.6
ADF	36.6	5.4
Ingredients (%)		
Maize		48.0
Sorghum		24.0
Barley		1.0
Soybean meal		3.5
Rapeseed meal		9.5
Wheat bran		6.0
Rice bran		5.0
Molasses		0.5
Calcium carbonate		1.4
Alfalfa meal		0.5
Sodium chloride		0.5
Dicalcium phosphate		0.05
Vitamin trace mineral premix		0.05

rates and saliva secretion volumes during the initial stages of feeding.

MATERIALS AND METHODS

Animals

Seven male goats (One Japanese Saanen goat, aged 6 yrs, weighing 72.5 kg; Six crossbred Japanese Saanen/Nubian goats, aged 4 to 6 yrs, weighing 72 to 97 kg) were used in this experiment. In order to collect parotid saliva, the apertura of one of the parotid ducts was surgically prepared to exteriorize it via the cheek of the animal more than 6 months prior to the experiment. Either an Atom Disposable Multiple Purposes Tube (o.d. 2.75 mm, 8 fr, Atom, Tokyo) approximately 10 cm in length or, depending on the animal, a fluid infusion tube (o.d. 4.00 mm, Terumo, Tokyo) was inserted into the parotid duct and fixed to the cheek. Furthermore, to enable the return of saliva collected from the parotid fistula, an extension tube (o.d. 4.50 mm, X3-50, Top, Tokyo) was inserted into the dorsal sac of the rumen. The other end of the tube was fixed to the skin. Parotid saliva flowing from the parotid fistula was collected in a plastic bucket. The goats were maintained in metabolic cages that allowed separate collection of urine, feces and saliva. The laboratory room was also maintained under thermoneutral conditions (25.0±0.2°C, 75.8±2.6% relative humidity).

The animals were fed twice a day at 10:30 and again at 16:00 for 2 h each time. Prior to the morning feeding, the collected saliva (3 to 5 kg) was infused into the rumen via the extension tube using a bathtub pump (Minipandy, KP-30F, Koshin, Tokyo). During the morning 2 h feeding period (10:30 to 12:30), the animals were fed 2 to 3 kg of roughly crushed alfalfa hay cubes. At 16:00 each day, the animals were fed again with 0.8 kg of alfalfa hay cubes, 200 g of commercial ground concentrate and 20 g of sodium bicarbonate. When the experiment was not in progress, the animals were given unrestricted access to water.

The composition and ingredients of the alfalfa hay cubes and ground concentrate feed are indicated in Table 1. Alfalfa hay cubes were ground with a Wiley mill (type 40-525 P, Ikemoto Rika Kougyou, Tokyo, Japan). The chemical components of the feeds were quantified using the procedures described by the Japanese Feed Association (Kato, 1988). The crude protein content was calculated from the nitrogen content of the feed, determined by a technique originally devised by Kjeldahl. The crude fat was determined by subjecting the feed to a continuous extraction with ethyl ether for 16 h using a Soxhlet's extractor. The crude fiber was determined by subjecting the residual feed from ether extraction to successive treatments with boiling sulfuric acid and sodium hydroxide of 5%. When the sum of the amount of moisture, ash, crude protein, crude fat and crude fibre was subtracted from 100, the difference was calculated as the nitrogen-free extracts (NFE). The acid-detergent fibre (ADF) and neutral-detergent fibre (NDF) were determined using techniques originally devised by Van Soest (1976).

Experiment

The experiments in this study were conducted according to a switchback design. Treatments in this experiment were carried out in order, beginning with the non-infusion control (NI) followed by the artificial mixed saliva intravenous infusion treatment (ASI) and concluding with the mannitol solution intravenous infusion treatment (MI). The treatments were carried out with 2 to 3 animals at 1 wk intervals to ensure that animals recovered and to minimize the compounding effects from the previous treatments. Respiration frequency, heart rate and rectal temperature were measured everyday prior to the morning feeding period. The values of these physiological parameters indicated whether an individual animal was in good health and had no measurable carry-over effects from the previous treatments.

One day before the commencement of each treatment stage in the experiment, polyethylene cannulae (o.d. 1.50 mm, No.5, Imamura Gomu, Tokyo) were inserted into the jugular veins on both sides of each goat. One was used for infusion, and the other was used for collecting blood samples. These cannulae were fixed in place and filled with

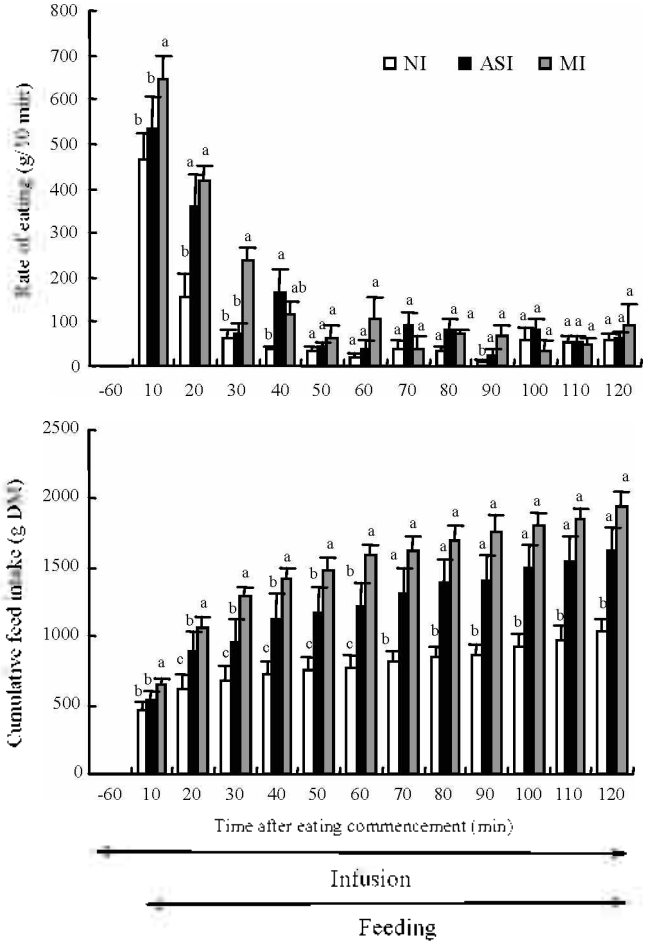

Figure 1. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol solution (MI) on feed intake and cumulative feed intake. Values are means±SE of 7 parotid fistulated goats. [a, b, c] Means with different superscripts differ. ($p<0.05$) from non-infusion treatment (NI).

heparin-saline (50 i.u./ml) to prevent coagulation of the blood. On the day of the experiment, the intravenous infusion of artificial mixed saliva or mannitol solution (17 to 19 ml/min) was conducted with a motor-driven pump (Cole-Parmer Instrument Co. PA-21, Chicago) over a 3 h period beginning 1 h prior to the commencement of morning feeding (09:30) and continued till the completion of feeding (12:30). The infusion rate for animals weighing 72.0 and 72.5 kg was 17.0 ml/min, while the rate for animals weighing 83 to 97 kg was 19.0 ml/min. The animals were deprived of water during morning feeding in each treatment. Eating rates were determined using a measuring scale. The alfalfa hay cubes (2.0 to 3.0 kg) were placed in a feed box attached to a 6 kg measuring scale. The weight of the remaining feed was measured every 10 min for the duration of the 2 h feeding period. Water intake was measured for 30 min following the completion of the 2 h feeding period. Fluid intake is regulated by thirst mechanisms (Guyton and Hall, 1996; Prasetiyono et al., 2000) and therefore the level of thirst (water appetite) in this experiment was evaluated quantitatively using water intake. Blood samples (5 ml) were collected through the polyethylene cannula into heparinized tubes. The blood was sampled at 09:30, 10:30, 10:45, 11:00, 11:15, 11:30, 12:00, 12:30, 13:00 and 13:15. Blood plasma was obtained by centrifugation (16,260×g, 10 min, 4°C).

The artificial mixed saliva, a solution resembling mixed saliva, consisted of 115 mM $NaHCO_3$, 5 mM KCl and 30 mM Na_2HPO_4. The mannitol (41.9 g) was dissolved in sterilized water (1 L). These solutions had osmolalities of 230 mOsm/L. The pH values of both solutions were adjusted to 7.4 by bubbling CO_2 gas (Blair-West and Brook, 1969; Sasaki et al., 1975). In preliminary experiments, the relationships between cumulative feed intakes over a 2 h period and infusion rates of 12 to 20 ml/min of artificial mixed saliva were examined. It was found that the optimum infusion rates of artificial mixed saliva to increase feed intake were 17 to 19 ml/min. Thus, these rates were adopted for this experiment. All surgical and experimental procedures were approved by the Animal Experimental Ethics Committee of the University of the Ryukyus and were in compliance with the Japanese code of practice for the care and use of animals for scientific purposes.

Biochemical analysis

Blood samples were placed in a hematocrit centrifuge (HC-12A, Tomy Seiko, Tokyo, 5 min, 16,260×g) to separate plasma and red blood cells. A hematocrit reader was used to determine hematocrit. Plasma total protein concentration and osmolality were measured using a refractometer (Atago, Tokyo) and an osmometer (OM-6010, Kyoto Daiichi Kagaku, Kyoto), respectively. The plasma concentrations of Na, K and Cl were measured using Spotchem EL (SE-1520, Arklay, Kyoto).

Statistical analysis

The experiments in this research were conducted according to a switchback design. A two-way analysis (animal, treatment) of variance was performed. After this, Duncan's Multiple Range Test was used to compare treatments. For statistical analysis, GLM procedure of SAS (SAS Inst., Inc., Cary, NC) was adopted. Data are presented as means±SE of the seven goats.

RESULTS

General physiological state

The mean values of respiration frequency, heart rate and rectal temperature before infusion in the three treatments were 18 breaths/min, 76 beats/min and 38.8°C, respectively.

Rate of eating and cumulative feed intake

Figure 1 shows the effects of intravenous infusion of artificial mixed saliva or mannitol solution on the rate of

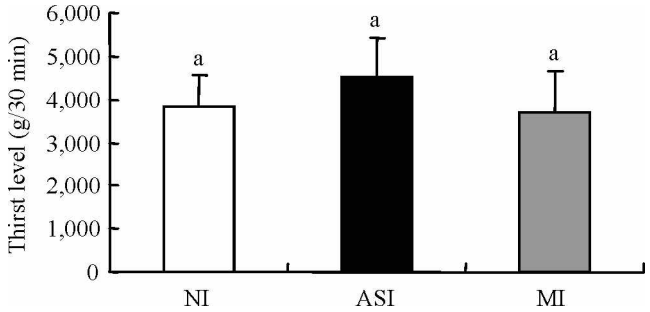

Figure 2. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol soluiton (MI) on thirst level. Values are means±SE of 7 parotid fistulated goats.

eating and cumulative feed intake. Eating rates in the NI treatment rapidly decreased in the first 30 min of feeding (0 to 10 min, 464 g/10 min; 20 to 30 min, 65 g/10 min). However, eating rates in the ASI and MI treatments decreased more slowly over the first 40 min than those in the NI treatment. Eating rates at 20 and 40 min after the initiation of feeding in the ASI treatment were higher than those in the NI treatment. Eating rates in the MI treatment during the first 30 min of feeding were higher than those in the NI treatment. After 50 min of the feeding period had elapsed, there was very little difference among the three treatments.

In comparison with the NI treatment (1,030±101.4 g/2 h), cumulative feed intakes in ASI and MI treatments were 56.6% (1,613±184.6 g/2 h) and 88.3% (1,939±121.0 g/2 h) greater ($p<0.05$) upon completion of the 2 h feeding period.

Thirst level

Figure 2 shows the effects of intravenous infusion of artificial mixed saliva or mannitol solution on thirst (water appetite) levels after the completion of the 2 h feeding period. Thirst levels in ASI (4,533±875.5 g/30 min) and MI (3,700±936.0 g/30 min) treatments were not significantly ($p>0.05$) different from that in the NI treatment (3,858±678.8 g/30 min).

Plasma osmolality, plasma total protein concentration and hematocrit

Figure 3 shows the effects of intravenous infusion of artificial mixed saliva or mannitol solution on plasma osmolality, plasma total protein concentration and hematocrit in the blood sampled at 60 min before feeding and 0, 15, 30, 45, 60, 90, 120, 150, 165 min after feeding had commenced. Plasma osmolality slowly increased in all three treatments over the course of 2 h feeding period. Compared with the NI treatment, plasma osmolality of the ASI treatment did not significantly differ in the first half of the feeding period, while the MI treatment caused a 2.8% increase (2.3 to 3.4%).

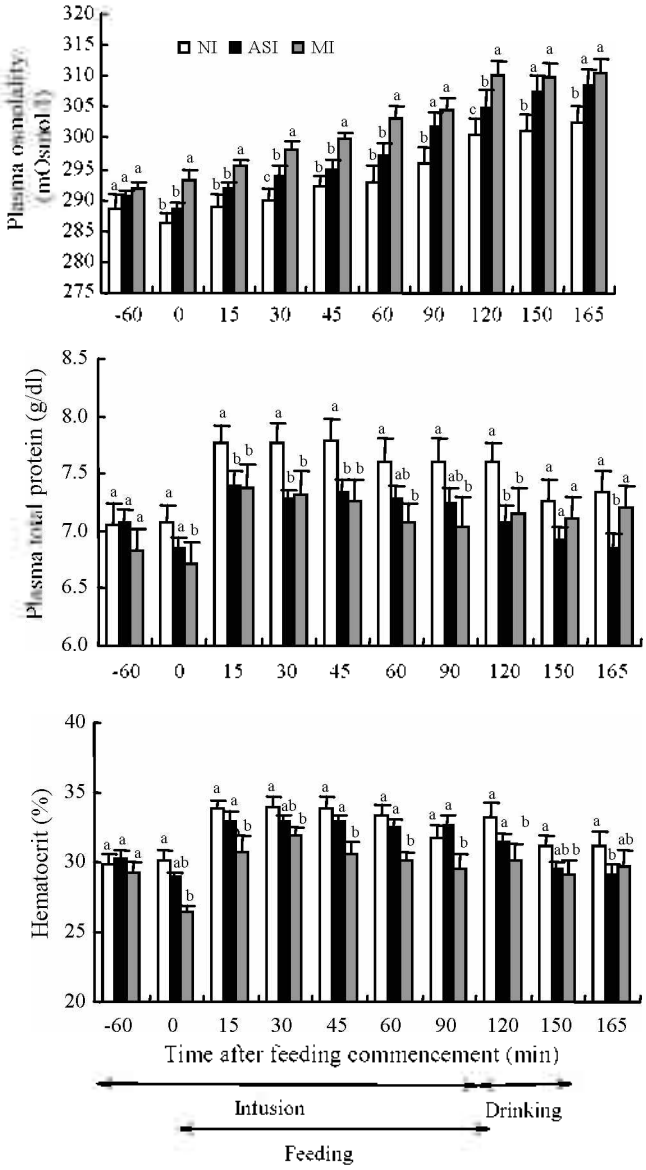

Figure 3. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol solution (MI) on plasma osmolality, plasma total protein concentration and hematocrit. Values are means±SE of 7 palotid fistulated goats. [a, b, c] Means with different superscripts differ ($p<0.05$) from non-infusion treatment (NI).

In all three treatments, rapid increases in plasma total protein concentrations were recorded during the first 15 min after the commencement of feeding. However, plasma total protein concentrations gradually decreased in all treatments for the remainder of the feeding period. In comparison with the NI treatment, during feeding the ASI and MI treatments decreased plasma total protein concentrations by 5.1% (3.3 to 6.8%) and 6.1% (5.0 to 7.4%), respectively.

All three treatments increased hematocrit markedly in the first 15 min after the commencement of feeding. Following this however, hematocrit gradually decreased in all three treatments for the remainder of the feeding period.

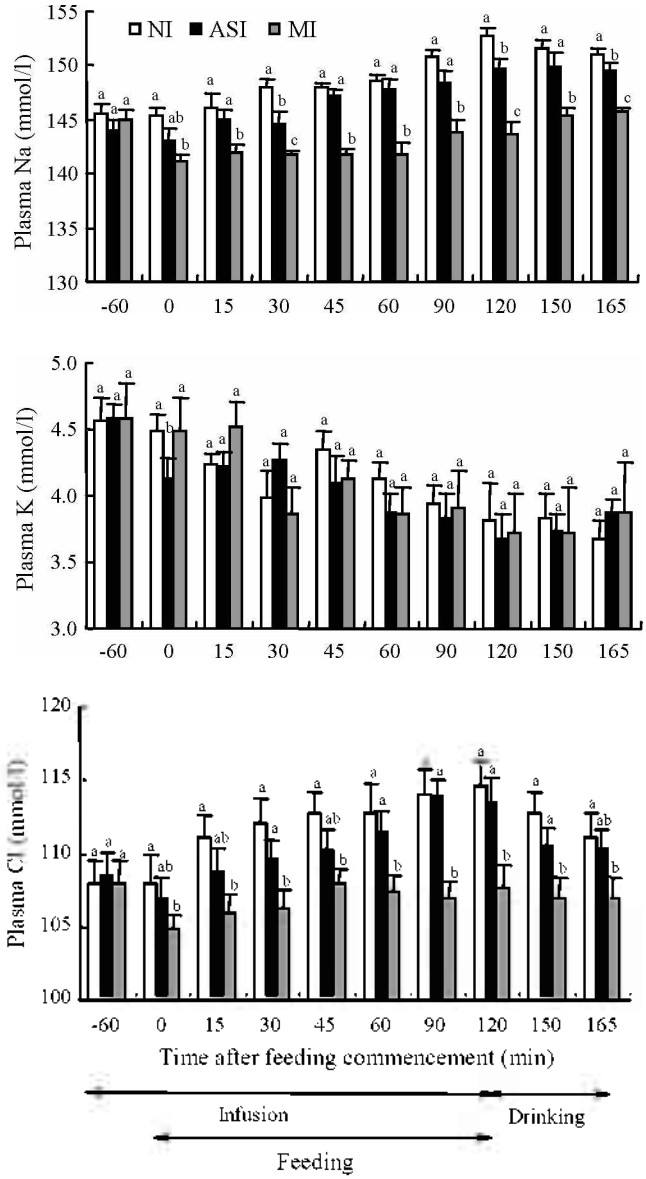

Figure 4. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol solution (MI) on plasma Na, K and Cl concentration. Values are means±SE of 7 parotid fistulated goats. [a, b, c] Means with different superscripts differ ($p<0.05$) from non-infusion treatment (NI).

Compared to the NI treatment, hematocrit of the ASI treatment did not significantly differ in the first half of the feeding period, while the MI treatment caused an 8.3% (6.2 to 9.3%) decrease.

Plasma concentrations of Na, K and Cl

Figure 4 shows the effects of intravenous infusion of artificial mixed saliva or mannitol solution on plasma concentrations of Na, K and Cl. Plasma Na and Cl concentrations in the three treatments increased slowly with feeding, while plasma K concentrations decreased. Plasma Na concentrations in the ASI treatment were not

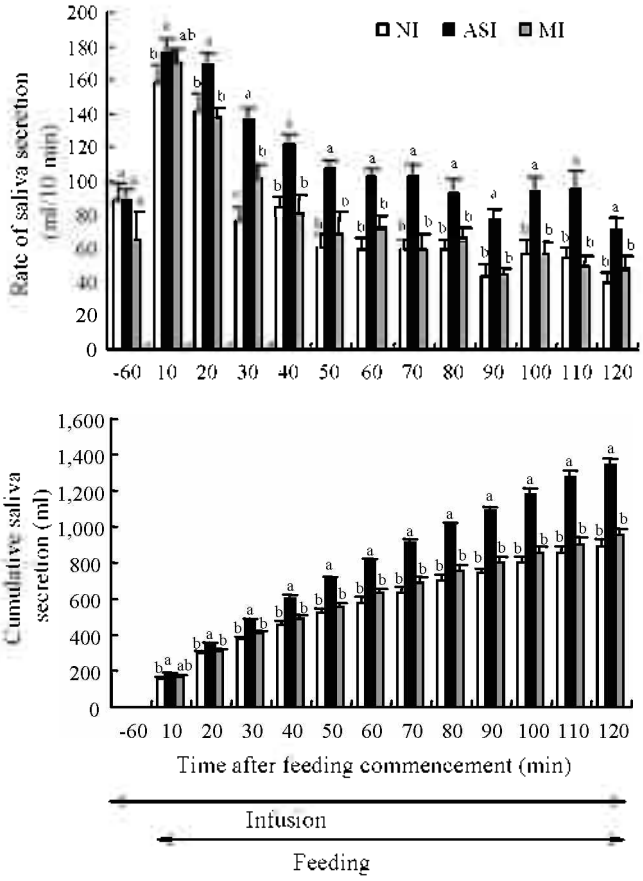

Figure 5. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol soluiton (MI) on rate of saliva secretion and cumulative saliva secretion. Values are means±SE of 7 parotid fistulated goats. [a, b, c] Means with different superscripts differ ($p<0.05$) from non-infusion treatment (NI).

significantly different from those in the NI treatment during feeding, while plasma Na concentrations in the MI treatment decreased significantly ($p<0.05$). Plasma K concentrations in the ASI and MI treatments were similar to those in the NI treatment. Plasma Cl concentrations in the ASI treatment were not significantly different from those in the NI treatment during feeding, while plasma Cl concentrations in the MI treatment decreased significantly ($p<0.05$).

Saliva secretion rates and cumulative parotid saliva secretion volume

Secretion rates of parotid saliva and cumulative parotid saliva secretions are shown in Figure 5. The rates of parotid saliva secretion in the three treatments peaked in the first 10 min after feeding was commenced (NI: before feeding 88±11 ml/10 min, 0 to 10 min 158±11 ml/min, ASI: before feeding 88±8 ml/10 min, 0 to 10 min 176±9 ml/min, MI: before feeding 65±16 ml/10 min, 0 to 10 min 169±9 ml/min). These rates then decreased as the feeding progressed. Saliva secretion rates in the ASI treatment

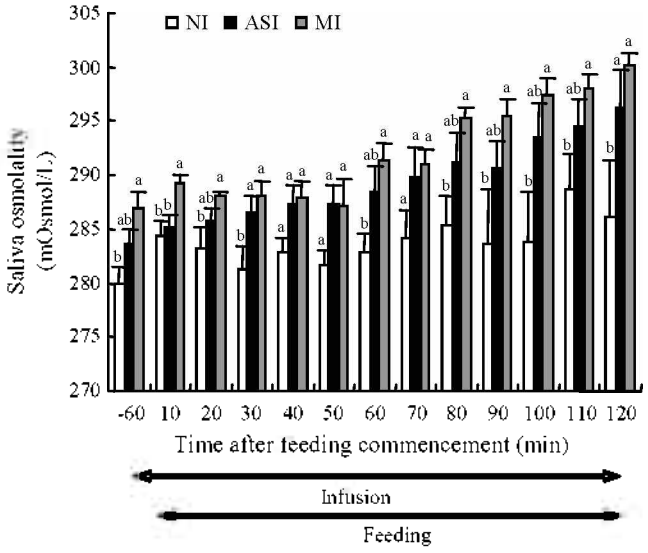

Figure 6. The effect of intravenous infusion of artificial mixed saliva (ASI) or mannitol soluiton (MI) on saliva osmolality. Values are means±SE of 7 parotid fistulated goats. [a, b] Means with different superscripts differ ($p<0.05$) from non-infusion treatment (NI).

slowly decreased until 80 min of the feeding period had elapsed, while the rates observed in the NI and MI treatments decreased more rapidly. The saliva secretion rates in the ASI treatments were markedly higher than those in the NI and MI treatments for the entire 2 h duration of the feeding period. In comparison with the NI treatment, saliva secretion rates in the MI treatment were significantly ($p<0.05$) higher at 30 min after the commencement of feeding.

Cumulative saliva secretion volumes upon conclusion of the 2 h feeding period were 893±36, 1,345±37 and 954±37 ml/2 h in the NI, ASI and MI treatments, respectively. Compared to the NI treatment, the ASI treatment increased cumulative saliva secretion volumes by 50.7%, but the values in the MI treatment did not change significantly.

Parotid saliva osmolality

Saliva osmolality in all three treatments increased slightly with feeding (Figure 6). Saliva osmolalities in the ASI and MI treatments were significantly higher than those in the NI treatment during feeding. Compared with plasma osmolality (Figure 3) in the NI treatment (286 to 310 mOsm/L), the values in saliva osmolality (280 to 300 mOsm/L) were lower.

DISCUSSION

Blair-West and Brook (1969) observed that sheep fed lucerne chaff once a day showed a marked reduction in plasma volume within 15 min of the commencement of feeding. In the NI treatment of the present experiment, a decrease in plasma volume estimated by increases in hematocrit and plasma total protein concentrations was apparent within 15 min of the commencement of feeding (Figure 3).

Table 2. Physiological parameters in goats prior to (NP) and after (P) parotid gland fistulation

	NP	P
Water intake (ml/day)	6,921±1,141	6,327±1,076
Urine excretion (ml/day)	5,441±910	4,477±847
Plasma osmolality (mOsm/L)	288.0±2.13	288.7±2.16
Plasma total protein (g/dl)	7.3±0.17	7.1±0.19
Hematocrit (%)	27.8±0.56	29.9±0.64
Plasma Na (mmol/L)	145.2±1.23	145.5±0.92
Plasma K (mmol/L)	4.6±0.09	4.6±0.17
Plasma Cl (mmol/L)	109.6±0.58	107.9±1.53

Parotid saliva flowing from the parotid fistula was collected in a plastic bucket. Prior to the morning feeding, the collected saliva was infused into the rumen via the extension tube using a bathtub pump. Values are mean±SE of 7 goats.

In comparison to the NI treatment, the level of increase in plasma total protein concentration brought about by feeding, was decreased by both the ASI and MI treatments (Figure 3). These results indicate that the level of decrease in plasma volume estimated by increases in plasma total protein concentrations declined significantly during the initial stages of crushed alfalfa hay cube feeding. The ASI and MI treatments in the present experiment replenished the fluid in the blood lost through accelerated saliva secretion during the early stages of dry forage feeding. In comparison to the NI treatment, increases in cumulative feed intake for the 2 h feeding period in the ASI and MI treatments were 56.6 and 88.3%, respectively (Figure 1). Prasetiyono et al. (2000) reported that there was a significant positive regression between plasma volume and feed intake in goats fed on dry forage. From these results, it is thought that the suppression of feed intake in goats fed on dry forage feed is not simply a result of rumen fill but also the result of hypovolemia caused by the accelerated secretion of parotid saliva during the initial stages of feeding.

Saliva is continuously lost in parotid fistulated sheep. Despite sheep being trained on a pedal-press system to allow them free access to a 0.6 mol/L $NaHCO_3$ solution and water, so long as the saliva lost through the parotid fistula was not returned to the rumen, sodium and water appetite in the fistulated sheep markedly increased while feed intake and urine volumes decreased (Sunagawa et al., 2002a). In the present experiment, in order to avoid any harmful influences on the animals, the saliva collected from the parotid fistula throughout the previous day was infused with a bathtub pump via an extension tube into the rumen prior to morning feeding. Among the goats used in this experiment, water intake and urine excretions recorded prior to parotid gland fistulation were not significantly different from values recorded after fistulation (Table 2).

There were also no significant differences recorded prior to and after fistulation in plasma osmolality, plasma total protein concentration, plasma sodium concentration. plasma potassium concentration and plasma chloride concentration (Table 2). These results indicate no change in the physiological state of the goats used in this experiment after fistulation.

Sato (1975) showed that the marked suppression of parotid saliva secretion following the conclusion of feeding in parotid fistulated sheep fed once a day on crushed alfalfa hay cubes is due to increases in plasma osmolality. Sato (1975) also reported that parotid saliva secretion in sheep was suppressed by intravenous injections of hyper-osmotic sodium chloride solution and hyper-osmotic mannitol solution. During the NI treatment in the present experiment. parotid saliva secretion volumes markedly increased with the commencement of feeding and then. despite the animals continued eating. dramatically dropped by the time 30 minutes of the feeding period had elapsed (Figure 5). Plasma osmolality increased slowly during feeding in the NI and ASI treatments (Figure 3) and was dependent upon (Figure 4) the continuous absorption of Na and Cl from the rumen (Stacy and Warner. 1966; Warner and Stacy. 1972). The present experiment attempts to clarify the factors involved in the suppression of parotid saliva secretion observed during feeding. As a result. in the first 1 h of the 2 h feeding period. plasma osmolality in the ASI treatment did not differ significantly from the NI treatment. Plasma osmolality in the MI treatment however. significantly increased. On the other hand. plasma total protein concentrations in both the ASI and MI treatments were significantly lower than the NI treatment (Figure 3). While plasma Na and Cl concentrations in the ASI treatment were similar to the NI treatment during feeding. they were significantly lower in the MI treatment (Figure 4). Parotid saliva secretion rates during feeding in the ASI treatment were higher than the NI treatment while the secretion rates recorded in the MI treatment were virtually the same as the NI treatment (Figure 5). In the MI treatment of the present experiment. the same volume of liquid as used in the ASI treatment. was infused to replenish the water lost from the blood in the form of saliva during the initial stages of feeding. However. the results indicate that the suppression of parotid saliva secretion during feeding is brought about by a decrease in plasma HCO_3^- concentrations caused by loss of $NaHCO_3$ from the blood. Thirst levels recorded following the conclusion of the morning feeding period remained unchanged by the intravenous infusion of artificial parotid saliva or mannitol solution (Figure 2). The reason for this is thought to be the fact that the intravenous infusion volumes of both artificial parotid saliva or mannitol solution were insufficient to compensate the thirst levels (Sunagawa et al.. 2001). The results of the present experiment prove that the humoral factors involved in the suppression of feeding and saliva secretion during the initial stages of feeding in goats fed on dry forage, are feeding induced hypovolemia and a decrease in plasma HCO_3^- concentration caused by loss of $NaHCO_3$ from the blood.

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